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# **Developing Best Practices for the Propagation and Restoration of Massive Corals: The Influence of Predation, Colony Size and Genotype**

Rivas, Nicolas I.

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UNIVERSITY OF MIAMI

DEVELOPING BEST PRACTICES FOR THE PROPAGATION AND RESTORATION  
OF MASSIVE CORALS: THE INFLUENCE OF PREDATION, COLONY SIZE AND  
GENOTYPE

By

Nicolas I. Rivas

A THESIS

Submitted to the Faculty  
of the University of Miami  
in partial fulfillment of the requirements for  
the degree of Master of Science

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Nicolas I. Rivas

Approved:

---

Diego Lirman, Ph.D.  
Associate Professor of Marine  
Biology and Ecology

---

Dalton Hesley, M.P.S  
Senior Research Associate  
Marine Biology and Ecology

---

Evan K. D'Alessandro, Ph.D.  
Lecturer and Director, M.P.S  
Marine Biology and Ecology

---

Guillermo Prado, Ph.D.  
Dean of the Graduate School

---

David Gilliam, Ph.D.  
Associate Professor of Marine  
and Environmental Sciences  
Nova Southeastern University

RIVAS, NICOLAS I. (M.S., Marine Biology and Ecology)  
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and Restoration of Massive Corals: The Influence  
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Coral reefs have undergone drastic declines due to a combination of human and natural disturbances. In response, restoration efforts were developed to recover lost ecosystem services. Over the past decade, reef restoration in Florida has focused almost exclusively on branching *Acropora* corals but declines in the abundance of corals with massive morphologies highlighted the need to expand our restoration toolbox and develop a holistic “multi-species” approach. Recent studies incorporating corals with massive morphologies into restoration have reported high mortality rates (>50%) because of predation by fish in the first few weeks following outplanting. To address this challenge, I conducted a series of experiments aimed at mitigating predation and understanding factors driving fish predation. I found limiting physical access to newly outplanted corals using colonies of the branching coral *Acropora cervicornis*, metal spikes, and cages to be highly effective at reducing predation impacts while in place but that cage and spike protective benefits declined immediately after their removal. I identified a size threshold where larger colonies ( $25 \text{ cm}^2$ ) are less susceptible to predation than smaller coral fragments ( $5 \text{ cm}^2$ ). I also found coral genotype to play a role in an outplant’s probability of being consumed or removed from the reef by fish, with the most susceptible genotype experiencing 86% mortality after 4 weeks compared to the least

susceptible genotype that experienced 26% mortality over the same period. Finally, I found evidence that the observed fish impacts are likely driven by consumption activities and not territorial behavior as dead coral controls were not impacted by fish while adjacent live corals experienced 100% mortality. These results suggest that preventing access by fish to coral outplants by planting them in close proximity to large, complex coral colonies, outplanting larger fragments, and utilizing multiple coral genotypes in restored reefs can be an effective way to limit predation impacts and improve the overall efficiency of reef restoration activities.

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## **Chapter 1. Introduction**

Over the past five decades there has been a rapid decline in the condition of coral reefs locally and globally (Wilkinson, 2008; Hughes et al., 2017). Coral reef projections estimate 90% of all reef locations to experience severe bleaching annually by 2055 and a 5% decline in calcification by 2034 (Hooidonk et al., 2014). The decrease in coral cover worldwide can be attributed to different stressors, with increased sea surface temperatures (SST) and disease (Miller et al., 2009; Heron et al., 2016) being particularly problematic recently. Rising sea surface temperatures (SST) due to global warming have triggered mass global bleaching events in 1998, 2010, and 2015/2016, with each event increasing in intensity (Wilkinson, 2008; Heron et al., 2016; Hughes et al., 2017). In 2005, the Caribbean experienced one of its worst mass coral bleaching and mortality events ever recorded, with about 80% of corals in the Caribbean basin having bleached and over 40% dying following the event (Eakin et al., 2010). Later, the 2015/2016 global bleaching event was determined to be one of the worst to date, with coral and other marine organism mortality recorded over thousands of square kilometers (Sully et al., 2019). In Florida, back-to-back bleaching events in 2014 and 2015 caused significant mortality to both wild and restored coral colonies (Drury et al., 2017). Such bleaching events have also been linked to outbreaks in coral disease that further decrease coral abundance (Muller et al., 2008; Miller et al., 2009; Gintert et al., 2019).

Coral diseases have been recorded as early as the 1970s, with the first published disease outbreak occurring as early as 1975 (Dustan, 1977). While coral diseases can be found globally, they have been especially prevalent in the Caribbean with approximately 76% of coral diseases described worldwide found within the Caribbean basin (Weil,

2004). An outbreak of white band disease in the late 1970s and early 1980s decimated coral populations in the Caribbean and led to the listing of *Acropora cervicornis* and *Acropora palmata* as threatened under the Endanger Species Act (NOAA, 2014), and later endangered by the International Union for Conservation of Nature (IUCN) (Aronson & Precht, 2001; Aronson et al., 2008; IUCN 2020). In 1995, another disease outbreak swept through the Florida Keys further depleting coral populations (Richardson et al., 1998). The disease, identified as “White Plague Type II”, was shown to affect 17 scleractinian corals at the time and now has been identified in over 41 different species of scleractinian coral (Richardson et al., 1998; Weil, 2004). Just ten years later, the 2005 bleaching event contributed to another drastic loss of coral populations via disease near the U.S. Virgin Islands (Miller et al., 2009). Most recently, a new disease known as Stony Coral Tissue Loss Disease (SCTLD) has spread through the Florida Reef Tract (FRT) leading to another 30% decrease in coral cover and 60% loss in live tissue cover (Precht et al., 2016; Walton et al., 2018; Muller et al., 2020). The focus of this study, the massive reef-building coral *Orbicella faveolata*, is one of the most susceptible species to SCTLD (Muller et al., 2020) and thus in pressing need for propagation and restoration.

Mass bleaching events and disease outbreaks are not the only factors that have influenced the state of the corals and reefs of the FRT. Cold-water anomalies (Lirman et al., 2011), pollution and sedimentation (Richmond et al., 2018; Cunning et al., 2019), eutrophication and algal overgrowth (Lapointe et al., 2019; Meyer et al., 2019), ocean acidification (Muehllehner et al., 2016), and hurricanes (Lirman & Fong, 1997) have also caused and exacerbated coral population declines on Florida reefs.

Around the world, reef restoration programs have been established to mitigate impacts and recover reef habitats and coral populations, (Rinkevich, 2005; Boström-Einarsson et al., 2018). Attempting to reverse coral reef decline through active restoration strategies is not a novel concept, with examples dating back to 1979 when the first attempts at transplanting coral took place (Birkeland et al., 1979). Since then, restoration methods have been improved and expanded globally to establish “Best Practices” to effectively restore reefs (Precht, 2006; Edwards, 2010; Johnson et al., 2011; Rinkevich, 2019). Most Caribbean restoration programs have focused on the propagation and outplanting of *A. cervicornis* and *A. palmata* due to their listing as endangered on the IUCN Red List, fast growth rates, and contribution to complex reef structure (Lemoine & Valentine, 2012; Lirman et al., 2014; Boström-Einarsson et al., 2018). The Caribbean is now home to over 85 different *Acropora* restoration programs, with six of those found in Florida and Puerto Rico (Young et al., 2012). Tens of thousands of acroporid corals are now outplanted onto Florida and Caribbean reefs each year (Lirman & Schopmeyer, 2016).

Unfortunately, while significant progress has been made in the restoration of *Acropora*, comparatively limited progress has been made with other coral species. The increasing sea surface temperatures, anthropological stressors, and disease events previously mentioned have continued to decimate coral populations of massive morphologies (Precht et al., 2016). Though acroporid corals grow quickly and provide complex reef structure, it is important to maintain levels of species diversity on reefs affected by multiple sources of disturbances (Brandl et al., 2019). Different coral species have been shown to have different levels of susceptibility to different stressors. Higher

species richness ensures that even large-scale disturbances will not result in complete reef destruction. Thus, focusing on a single coral taxon makes restored reefs susceptible to disturbance events such as hurricanes that affect branching corals disproportionately. In contrast, massive corals have been determined to be more resilient to physical impacts, heat stress, and anthropological stressors ( Loya et al., 2001; McClanahan, 2004; Wagner et al., 2010; Lirman et al., 2011). This highlights the need for a multi-species approach in reef restoration that includes corals with diverse morphologies and stress susceptibilities.

The active restoration of massive corals, however, has proven challenging due to their slow growth rates (0.2-1 cm/year) (Forsman et al., 2015). In 2014, a process known as “microfragmentation” opened the possibility of growing massive corals at accelerated rates and ecologically meaningful scales (Page et al., 2018). Microfragmenting consists of carefully dividing massive coral colonies into small,  $\sim 2.5\text{cm}^2$  pieces. Fragmenting these large, individual colonies into multiple small colonies has shown to increase individual growth rates 2-7x what they would grow naturally (Page et al., 2018). Microfragmentation allows restoration practitioners around the world to propagate hundreds of corals in a confined space to grow and outplant. While strides have been made in propagating massive corals, achieving high levels of survivorship post-outplanting continues to be a limiting factor in scaling up massive coral restoration. Small coral outplants may be outcompeted by macroalgae, which in turn may attract grazers that not only feed on the macroalgae, but on the corals as well (Miller & Hay, 1998). Such grazing habits have also been observed to affect post settlement success of stony coral (Christiansen et al., 2009). Fish corallivory has been identified as a major

bottleneck in massive coral restoration success and population recovery (Jayewardene et al., 2009; Koval et al., 2020).

Reef fish play a critical role in maintaining a healthy coral reef ecosystem (Plass-Johnson et al., 2015). Grazing by herbivorous fish has been documented as a key factor keeping algal populations on reefs at bay (Adam et al., 2015). If left unchecked, increased algal cover can have negative effects on coral recruitment, growth, and survivorship (Miller & Hay, 1998; Lirman, 2001; Kuffner et al., 2006). While fish families such as Chaetodontidae, Labridae, Monocanthidae, and Scaridae are primarily known for grazing and feeding on algae, they can also feed on corals (Miller & Hay, 1998; Cole et al., 2008; Steneck et al., 2014). The exact mechanism(s) driving reef fish to target coral outplants are unknown, however. Studies on fish corallivory have identified species-specific differences in corallivory, where different species of parrotfish preferred certain species of coral over others (Burkepile et al., 2019). Speculations also suggest that fish may be attracted to the endolithic algae found within coral skeletons, or may be attacking the outplanted corals as part of territorial or marking behavior (i.e., parrotfish, damselfish, triggerfish), viewing the outplants as “intruders” (Mumby & Wabnitz, 2002; Gibbs & Hay, 2015). Here, I explore whether fish target coral outplants while feeding or as part of their territorial behavior by outplanting both live and dead corals. I hypothesized that both dead and live corals would be targeted equally if fish are removing intruders from their territories.

With decreasing coral populations, the role and impact of corallivorous fish has been widely debated. Corals in the Caribbean, as previously mentioned, are already exposed to a wide variety of stressors. Predation can deplete stored energy reserves and

act as a vector for disease (Meesters & Bak, 1993; Raymundo et al., 2009; Schoepf et al., 2013; Nicolet et al., 2018). Page et al. (2018) noted that coral colonies that suffered over 40% tissue loss via predation were more likely to undergo complete mortality. Nevertheless, the overall positive impacts of herbivorous fish continue to outweigh the negative(s) at reef scales (Mumby, 2009). Without herbivorous fish, phase shifts from coral-dominated reefs to algal-dominated would occur (Lirman, 2001; Hughes et al., 2007). This net positive, however, does not consider the high mortality rates from predation recorded in Koval et al. (2020) (Fig. 1), which highlights the need to mitigate predation, preferably without increasing algal overgrowth susceptibility on fragments being outplanted for restoration.

Assuming a finite number of corals are available for collection (especially those of threatened species), propagation, and restoration, restoration practitioners are faced with the option of outplanting a few large coral colonies or a larger number of smaller, fragmented corals. Tradeoffs between colony size, growth rates, and predation survivorship are all factors that need to be considered in this decision (Page et al., 2018; Lustic et al., 2020). Page et al. (2018) observed smaller fragments were more susceptible to predation and mortality than larger colonies. When outplanted colonies suffered >40% tissue loss, comparable to a single bite by a large parrotfish on a small microfragment, they were not able to recover. However, when coral colonies with >40% predation were excluded from analysis, growth rates were significantly higher in the smaller colonies. These quick growth rates on smaller microfragments can be used to encourage fusion between coral colonies to create a larger colony less susceptible to predation (Forsman et al., 2015). In contrast to the predation patterns recorded by Page et al. (2018) and Koval

et al. (2020), a recent study by Lustic et al. (2020) found that medium-sized (40-130 cm<sup>2</sup>) colonies of *Orbicella faveolata* and *Montastraea cavernosa* outplanted onto a reef in the Florida Keys showed no significant impacts of fish predation, suggesting a potential size threshold for predation-impacts. Here, I compare predation impacts on isolated (~5 cm<sup>2</sup>) and clustered (~25 cm<sup>2</sup>) fragments to determine whether it is beneficial to outplant larger (but fewer) coral ramets.

Fish corallivory has also been documented to affect a wide range of species. Various studies have identified interspecific differences in palatability indicating that fish may actively select their coral prey (Miller & Hay, 1998; Rotjan & Lewis, 2005; Koval et al., 2020; Quimpo et al., 2020). While predation by snails or worms has been identified as a source of outplant mortality in *A. cervicornis*, these are commonly slow processes that have chronic impacts over long periods of time (Young et al., 2012). Williams et al. (2014) identified that corallivorous snails can target *A. palmata* preferentially. Based on previous observations, fish grazers or corallivores avoid newly planted *A. cervicornis* but instead target outplanted fragments of corals with massive morphologies (pers. obs.). Preferential selection between species emphasizes the need to mitigate predatory effects on certain corals used in coral restoration, however, little is known about the intraspecific differences in palatability. Prior research has shown that coral genotype has a strong and relative influence on phenotypes such as growth and disease susceptibility (Lirman et al., 2014; Manzello, et al., 2017; Miller et al., 2019). Here, I examine the potential role that coral genotype may have on susceptibility from predation. Identifying genotypes and phenotypes that are less susceptible to predation would allow practitioners to successfully restore reefs that have high abundances of fish that target massive coral outplants.

The purpose of this study was to develop methods for outplanting massive corals that would mitigate predation and therefore increase survivorship. The overall success of coral restoration depends on obtaining a more complete understanding of how reef organisms interact with outplanted corals. If outplant survivorship is increased with a proper mitigation strategy, and outplant techniques and genotypic influences are better understood, then restoration programs may begin to outplant at larger scales with increased efficiencies. I hypothesized that outplant survivorship could be increased if predation rates were mitigated during the initial outplanting period. This was because predation rates on fragmented outplants seem to peak in the first month post outplanting (Koval et al., 2020). The effect of outplanting fragments close together to resemble a larger colony was also studied. I hypothesized that fragments outplanted as a cluster would be less susceptible to predation due to their larger combined size. Predation susceptibility of corals of the same species but different parent colonies (i.e., genotypes) was also evaluated. I hypothesized that predation impacts would vary among genotypes based on palatability. Finally, I explored the mechanisms driving fish predation on coral outplants. Previous studies have suggested that some parrotfish species target corals outplanted within their territories causing significant tissue damage (Francini-Filho et al., 2008; Rotjan & Lewis, 2009). To evaluate whether the predation impacts observed previously by Koval et al. (2020) at Flamingo Reef were due to consumptive or territorial behavior (i.e., removal of foreign objects within established territories), I added a set of dead-coral controls to the predator exclusion and genotype effects experiments. I hypothesized that if the main driver of coral mortality is tissue consumption, dead

controls would be avoided by fish predators. Conversely, if territorial behavior is the key driver, I expected both live and dead corals to be removed at similar rates.

## **Chapter 2. Methods**

### **2.a. Study Species and Site**

This study was conducted between February and April 2020 on a single reef (Flamingo Reef; 25.70° N, 80.09° W, max depth = 7.5 m) in Miami, Florida, US (Fig. 2). This site was selected due to previous studies reporting high survivorship (92%) of staghorn outplants, high abundance of corallivorous fish, and high levels of fish predation on outplanted massive corals (Koval et al., 2020). A reef with high fish predation was crucial to allow significant differences to be identified.

This study involved two species of coral: *Acropora cervicornis* (staghorn coral) and *Orbicella faveolata*. *O. faveolata* was selected as the study focus due to its status as threatened in Florida under the US ESA (Smith & Island, 2014), importance as a reef builder (Ginsburg et al., 2001), and available stock and genotypic diversity within the University of Miami (UM) coral restoration program. A single, large (50 cm in diameter) colony of *O. faveolata* was collected from a sea wall in Key Biscayne, FL. A diamond band saw was then used to fragment this colony into small, ~4cm<sup>2</sup> fragments. Individual fragments were labeled and attached to ceramic plugs (commonly used in the aquarium trade) using super glue (Gorilla Glue) as described by Page et al. (2018) (Fig. 3). The plugs were deployed at the UM in-situ coral nursery for at least 3 months for recovery and acclimation before being used for this experiment.

## 2.b. Protection by *Acropora*

Nursery-grown *A. cervicornis* corals previously outplanted at Flamingo Reef by the UM coral restoration program (Lirman et al., 2014) were used as a treatment to protect or deter fish predation on outplanted fragments of *O. faveolata*. Due to the complex structure of *A. cervicornis* colonies, we hypothesized outplanting massive coral fragments in proximity to *A. cervicornis* could act as a physical barrier and/or as a “deterrent” species. This is similar to the use of companion planting on crop fields or gardens where plants are grown together to mask chemical cues that may attract predators and/or to make it more difficult for specialized predators to “find” their target (Root, 1973; Parker et al., 2013).

Three previously established staghorn coral restoration plots at Flamingo Reef were used for this experiment. Each of these circular plots were established in 2018 and have 95 - 120 staghorn corals (max diameter ~25 cm) within a 5 m<sup>2</sup> area (Fig. 4), providing a dense staghorn population for this study. Within each of these three plots, 36 fragments of *O. faveolata* (5 cm<sup>2</sup> each) were outplanted with cement at tiered distances from staghorn colonies. A cement mixture of 1-part Portland cement and 0.1 parts Silica fume (Unsworth et al., 2020) was prepared and deployed as dollops (circumference = 22 cm) using decorator piping bags. The *O. faveolata* fragments were then fixed to the reef in the cement dollops. Twelve fragments were located immediately adjacent to the bases of staghorn colonies (Fig. 5), 12 fragments were outplanted 25 cm away from the staghorn colonies, and the last 12 were outplanted at 50 cm away from the staghorn colonies to serve as distant controls (Fig. 6). This was replicated at each of the three staghorn plots for a total of 108 *O. faveolata* outplants.

## 2.c. Predator Exclusion

Caging has been used in the past to study factors such herbivory and competition between macroalgae and corals (Lirman, 2001; Suchley & Alvarez-Filip, 2017). However, cages have also been used to protect corals from predatory fish (Miller & Hay, 1998; Hughes et al., 2007). For this study, cylindrical cages (height = 11 cm, diameter = 10 cm) were built using 1.25 cm galvanized mesh and deployed as a physical barrier to protect coral outplants from reef fish. Seventy-two *O. faveolata* fragments from the same colony used for “Protection by *Acropora*” were outplanted between three additional reef plots (10 m in diameter) at least 10 m away from any *A. cervicornis* colonies. Each “Predator Exclusion” plot received 24 *O. faveolata* plugs outplanted using cement as described previously, with half (n=12) outplanted inside full cages and the other half (n=12) outplanted within open cages (no top) to serve as controls for water flow and light (Fig. 7). All cages were secured to the reef using masonry nails and tracked with a numerical tag. This setup was replicated at all three reef plots. Cages were cleaned periodically if algal overgrowth was observed.

Metal spikes were used as an additional Predator Exclusion treatment to prevent access to the coral outplants by predatory fish. Steneck et al. (2014) used pegs to deter fish predation on *Porites* and *Agaricia* coral recruits and found a significant reduction in bite marks from large parrot fish when compared to controls without peg protection. As such, spikes were hypothesized to function as a physical barrier that could prevent coral predation and/or removal during the initial high predatory period.

To investigate this, cement pucks (n = 36, diameter = 10 cm) were hand-molded and fixed with six “spikes” along with a numerical tag for tracking and then left to cure

for 24 hours. Spikes (10 cm in height) were made from galvanized steel mesh. Coral fragments ( $5 \text{ cm}^2$ ), of the same genet, were then fixed into the center of the cement pucks using additional cement (Fig. 8). Twelve of these cement pucks were then cemented within each of the same three Predator Exclusion plots used for the cages. In addition, 12 fragments on ceramic plugs with no physical protection were outplanted with cement at the same time as cage and spike deployments at each of the three reef plots to serve as controls (Fig. 9).

Because predation rates seem to decrease after the first month following outplanting, cages and spikes were removed at the one-month (four week) time interval (Koval et al., 2020) (Fig. 10). To ensure that fish attention and/or predation was not enhanced due to increased algal presence within the full cages (as shown by Miller and Hay, 1998), cages were lifted so algae and sediments could be removed using a metal wire brush. Cages were then reattached until sediment and algal filaments had settled (~60 min), at which point the cages were completely removed. To investigate potential habituation of the newly exposed corals, 27 new *O. faveolata* fragments ( $5 \text{ cm}^2$ ), of the same genet, were outplanted within three new reef plots located 3 meters away from the associated Predator Exclusion plots at the same time of the cage and spike removal.

#### **2.d. Size Influence**

The influence of outplant size on predation was also investigated here. Recent studies of outplanted corals in Florida noted decreased levels of predation on larger fragments (Page et al., 2018) as well as minimal predation on medium-sized corals (Lustic et al., 2020). Thus, I hypothesized that placing corals in a close arrangement

would resemble a larger colony and reduce the impact of predation by reef fish compared to small corals planted individually.

To test the influence of size on predation, I deployed fragments as individuals ( $5\text{ cm}^2$ ) as well as clusters of 5 individuals placed closely together to encourage fusion and resemble a larger *O. faveolata* colony of  $\sim 25\text{ cm}^2$  (Fig. 11). Three new reef plots at least 10 meters from the already established plots were set up with five large colonies outplanted per reef plot ( $n = 15$ ). In addition, 12 individual *O. faveolata* fragments ( $5\text{ cm}^2$ ), of the same genet, were outplanted within each of these three reef plots (total of 36 *O. faveolata*) to compare the success of small and large colonies.

### **2.e. Genotype Influence**

To test the influence coral genotype may have on susceptibility to fish predation, five different genotypes (“FB”, “FE”, “KA”, “SA”, “PA”) of *O. faveolata* were utilized. One of the genotypes tested, “KA” was the genotype used in all the previously described experiments. Colonies were collected from the UM coral nursery, fragmented, and fixed onto ceramic plugs using the same methodology previously described. In total, 36 *Orbicella faveolata* fragments (size =  $5\text{ cm}^2$ ) of each genotype ( $n=5$ ) were prepared for outplanting. Three new reef plots (diameter = 10 m) were established for this Genotype Influences study. These plots were at least 400 feet away from the other research plots and 10 meters from each other. The *O. faveolata* corals were outplanted via cement in groups of six, containing one fragment of each genotype ( $n=5$ ) and a dead control fragment.

Each group of corals were placed in a circle, with 12 inches between each fragment and the dead control in the center (Fig. 12), for a total of 12 sextets per plot (n=3) (Fig. 12).

#### **2.f. Role of Territoriality**

To investigate the role of territoriality, a large colony of *O. faveolata* that died in prior stress experiments was fragmented as previously described to create dead coral control fragments. These were fixed to ceramic plugs using super glue and painted with REVLON nail polish to resemble live coral color (Fig. 13). Nine dead control fragments were outplanted in each of the three plots (27 total) where the additional living fragments were outplanted at the time of the removal of the cages and spikes (Fig. 10). In addition, 12 dead controls were deployed in each of the three Genotype Influences plots (36 total). Dead controls were assessed for presence/absence as well as predation impacts (% tissue mortality / paint removal) during each survey. Two weeks after outplanting the dead controls, an additional 24 live *O. faveolata* coral fragments were outplanted adjacent to the dead controls to account for possible deterrent effects from the nail polish.

#### **2.g. Video Observations**

Video cameras (n=3) set to record for 12- to 24-hour periods were deployed at the one- and two-week time points throughout both studies to identify fish species that were interacting with the coral outplants. One camera was set to record overnight using a diving flashlight attached to the video camera emitting a red light (~600-700 nm) (Fig. 14). Video was analyzed after each collection by sifting through recordings and

identifying which species of fish directly interacted with the coral outplants, either through predation, grazing, or otherwise.

## **2.h. Monitoring and Analysis**

Every individual fragment was surveyed one week, two weeks, and four weeks after deployment. Corals in the cage and spike treatments were also monitored one week after cage and spike removal (i.e., after 5 weeks). For all individual fragment outplants (i.e., controls, *Acropora* protection, predator exclusion, genotype, and territoriality experiments), I recorded the presence/absence of each outplanted coral as well as the number of corals with 100% tissue removal to calculate the coral mortality proportion. This included both physical removal and 100% tissue mortality caused by predation. For the size experiment, I recorded both the mortality proportion as just described and the proportion of the coral tissue (single fragment and fragment clusters) removed by predation within surviving corals. All observations were made in situ.

The proportion of corals removed by predation and with 100% tissue mortality was compared among plots, treatments, and survey time points for each experiment using a Generalized Linear Model (GLM) as described by Warton and Hui (2011). A GLM with binomial distribution and a logit link function was used to quantify and assess the probability of outplant removal (Koval et al, 2020). Tukey post hoc tests were used to evaluate pairwise differences among the levels of the categorical variables in the models (plots, treatments, time). A t-test was used to compare the proportion of tissue removed by predation relative to colony size. small/individual colonies and larger (cluster)

colonies. The goal of this comparison is to determine whether, on a cm<sup>2</sup>-basis (i.e., normalized by initial size), more or less coral tissue is removed from small or large coral outplants.

## **Chapter 3. Results**

Four types of predation were observed on outplanted corals; 1) no tissue mortality (Fig. 15a), 2) partial tissue mortality (Fig. 15b), 3) complete tissue mortality (Fig. 15c), and 4) complete removal (Fig. 15d) of the coral fragment from the reef. No significant effect of plots ( $p > 0.05$ ) was documented within experiments and thus removal data were combined for all plots in each experiment (Table 1).

### **3.a. Protection by *Acropora***

Staghorn colonies in this study provided protection from predation. *O. faveolata* outplants that were placed directly adjacent to staghorn colonies experienced significantly less predation mortality ( $p < 0.05$ ) than corals located 50 cm away (Fig. 16). Colonies placed at 25 cm showed lower mortality compared to those placed at 50 cm, but this difference was not significant ( $p = 0.54$ ). By the end of the study, corals outplanted adjacent, 25 cm away, and 50 cm away from a staghorn colony experienced 64%, 86%, and 92% mortality, respectively. Predation impacts increased significantly (Tukey HSD,  $p < 0.05$ ) between the beginning and end of the study, with the majority of predation occurring between weeks 1 and 4 (Table 1). No disease or mortality from other factors were recorded.

### **3.b. Predator Exclusion**

After four weeks, closed cages had 100% coral survivorship, showing complete predator exclusion and no impacts on coral health. Conversely, open cages and spike treatments showed increasing levels of mortality over that same time (75% and 19%,

respectively), illustrating that fish predators were able to access the corals. There were, however, significant differences in probability of mortality between closed cages, open cages, spike treatments, and control fragments ( $p < 0.05$ , Tukey HSD,  $p < 0.05$ ), and the probability of mortality increased significantly over time ( $p < 0.05$ ). Control fragments had the significantly highest probability of mortality, with 100% of corals lost after 4 weeks (Fig. 17).

After four weeks of protection, the cages and spikes were removed and, at the same time, 9 live control and 9 dead controls were outplanted within new plots ( $n=3$ , 27 live and 27 dead controls total) (Fig. 10). One week after removing the Predator Exclusion treatments, 97% of corals previously placed inside open cages, 78% of corals under closed cages, 72% of corals previously protected by spikes, and 96% of live controls suffered complete mortality (Fig. 18). Dead controls had 100% retention with no signs of predation (i.e., feeding scars). One week post-removal, the closed cage, spikes, and live control treatment outplants had a significantly higher probability of mortality than the outplants originally placed in the open cage treatment ( $p < 0.05$ ).

### **3.c. Size Influence**

Probability of mortality was significantly influenced by outplant size (Table 1). Probability of mortality was significantly higher on small coral outplants compared to “large” outplant clusters ( $p < 0.05$ ) (Fig. 19). This was the only experiment where no mortality was observed on the first week after outplanting, but probability of mortality increased significantly over time ( $p < 0.05$ ).

On average, outplanted colonies lost significantly more tissue per cm<sup>2</sup> when planted individually than when clustered as a single colony (t test, p < 0.05).

### **3.d. Genotype Influence**

Significant differences in the probability of mortality due to fish predation were found among the five *O. faveolata* genotypes deployed as small fragments (p < 0.05; Fig. 20). Genotype KA had the highest probability of mortality compared to the other genotypes, which did not differ significantly from each other (Tukey HSD, p < 0.05) (Fig. 20). Predation rates increased significantly between the one-week to two-week period but decreased thereafter. Only 2 of the 36 dead controls experienced complete “mortality” (i.e., complete nail polish removal).

### **3.e. Role of Territoriality**

Of the 63 fragments deployed as dead-coral controls, only 5% showed signs of fish predation as evidenced by fish bites and none were physically removed. A week after the deployment of live fragments adjacent to the dead controls, 100% of the live fragments had either been completely consumed or removed.

### **3.f. Video Observations**

Video cameras deployed throughout plots failed to capture active removal or complete predation of outplants, but a variety of species were observed to directly interact and “nibble” on the outplanted colonies (Table 2).

## **Chapter 4. Discussion**

Fish-predation impacts on outplanted fragments of the threatened coral *Orbicella faveolata* at a reef in Miami, Florida, US, were very high, with outplanted coral fragments experiencing >80% mortality over 4 weeks. While these high predation impacts are a serious concern for reef restoration, I identified here important factors that significantly influence the probability and rate at which fish predation occurs, which can be used to refine future outplanting methods to enhance the restoration efficiency of massive coral taxa.

Placing *O. faveolata* outplants adjacent to staghorn colonies with branching morphology significantly reduced the probability of mortality by fish predation, indicating that restoring multi-species assemblages can provide synergistic benefits to the species restored. This reduction in predation observed is likely due to the complex structure of *Acropora* and its ability to physically prevent fish from reaching the outplants, supporting the hypothesis that staghorn colonies act as a physical barrier (Lemoine & Valentine, 2012). While massive corals may fair better in the short-term under the physical protection provided by *Acropora*, *Acropora* may outcompete and smother the smaller, slower growing outplants over time and therefore may not be as effective as a longer-term protective barrier. Nevertheless, the average mortality (81%) observed within the *Acropora* plots was still lower than the mortality levels observed on control plots without staghorn corals. This suggests outplanting multiple species together or outplanting onto reefs with high species richness may protect coral outplants by masking the presence of the smaller coral outplants to fish predators, providing relief until corals reach a size refuge against predation as documented in Lustic et al. (2020).

I further investigated the potential benefit of physically protecting small coral outplants using cages and metal spikes. Closed cages prevented any meso- and macro-predators from feeding on outplanted corals. Outplants in the spike treatment experienced a low (~20%) mortality rate before spike removal, likely due to the inability of larger fish (i.e. parrotfish) to go through or reach the outplant. Open cages provided some protection but still lost 55% more outplants than spikes, possibly due to the larger opening (6 cm on spikes vs 13 cm on open cages). Thus, physical protection, can be effective in mitigating predation on outplanted coral colonies. However, I showed that the protective benefits quickly disappear after the physical barriers are removed as corals were quickly consumed during the first week after removal. Habituation of fish to new objects within their habitat did not mitigate predation impacts once cages or spikes were removed. Thus, providing a temporary relief from predation does not appear to be an effective long-term method to protect outplants under high-predation conditions. While protective methods such as cages can be deployed for longer periods to allow for corals to grow and maybe reach a size refuge, the frequent cleaning required to keep these barriers free of macroalgae as well as the competition from macroalgae that corals can experience inside the cages make this approach impractical over long periods. Minimal algal growth was observed around outplants surrounded by spikes before removal, likely due to the ability of smaller grazing fish to feed around the spikes and coral (Adam et al., 2015). Developing a protection method using spikes made of biodegradable materials could potentially provide early protection while also allowing corals to reach a size refure before the protection afforded by the spikes is lost and may be a viable long-term alternative to caging.

Restoration practitioners have the option of outplanting several small fragments or fewer larger colonies (Page et al., 2018). Here, corals clustered together ( $25\text{ cm}^2$ ) suffered less proportional mortality than smaller fragments ( $5\text{ cm}^2$ ) planted individually, suggesting a protective size threshold that was also observed by Page et al. (2018) and Lustic et al. (2020). Thus, under high predation, it is beneficial to plant fewer but larger corals. The role of clustering smaller fragments together, similar to this experiment, compared to outplanting one single larger fragment should be further explored to look for tradeoffs in growth rates and survivorship.

Genotype played an important role in determining the survivorship of outplanted corals. The “KA” genotype used for all experiments was also the most susceptible to fish predation, suggesting intraspecific variations in palatability among genotypes. While the potential reasons behind these differences were not directly evaluated, future studies should evaluate the factors influencing prey choice by fish predators such as skeletal properties, polyp accessibility, and nutritional composition among coral genotypes that may attract or deter a predator as suggested by Brooker et al. (2013). Clearly, genotypes with high palatability should not be planted in habitats or sites with high levels of fish predation, suggesting a quick genotype screening experiment may need to be conducted when restoring high-predation sites. Genotypes that experienced less predation in comparison to genotype “KA” still experienced relatively high mortality rates (26%-39%), emphasizing the need to develop effective methodologies to increase outplant survivorship. The mortality rates of the other, less palatable or less targeted genotypes was still substantially lower than those observed in our other experiments despite not having any physical protection. Therefore, I believe increasing outplant diversity, both

inter- and intra-specifically, combined with the predation mitigation techniques explored would most likely result in increased survivorship.

While 85% of outplants underwent complete mortality and/or removal in our study and the video recorded various fish species interacting with our outplants (Table 2), no direct visual or video evidence of coral removal was recorded. Nevertheless, I believe that the removal of corals can be attributed directly to fish predation. Coral fragments kept at the UM Nursery (where no fish predators have been observed) using the same adhesion method experience no removal, eliminating suspicions of adhesive failure. Furthermore, outplanted dead-control fragments ( $n=63$ ) experienced minimal predation (5%) and no removal in our study. If fish were removing outplants out of territorial behavior I would have expected similar removal and/or mortality rates as the live outplants or significant differences in probability of mortality between plots (Gibbs & Hay, 2015). Additionally, all live coral fragments outplanted directly adjacent to the painted controls were completely consumed or removed while the painted controls remained untouched, suggesting that the active predation and removal of live fragments is not due to attachment failure or a territorial behavior but rather predator-prey interactions (Brooker et al., 2013; Gibbs & Hay, 2015).

## **Chapter 5. Conclusions**

The results of this study highlight a serious bottleneck in the success of massive-coral restoration that needs to be addressed prior to the expansion of this practice as the high mortality values (84%) recorded here are clearly not sustainable. While the mortality values recorded may be unusually high due to the abundance of fish predators at the selected reef site, as well as, the unexpected palatability of the *O. faveolata* genotype used in this study, if these mortality values are replicated elsewhere in Florida, the cost of restoration would clearly exceed its benefits. Nevertheless, my study documented steps that can be taken to reduce predation impacts. These steps include: 1) evaluating potential predation pressure by conducting fish surveys at candidate sites, 2) screening coral genotypes for palatability prior to full deployment, 3) outplanting corals within multi-species plots that afford physical protection, 4) designing an efficient long-term barrier that may allow corals to reach a size refuge against predation without excess required maintenance, and 5) outplanting larger corals, fragments clusters, or allowing smaller coral fragments to fuse within nurseries prior to outplanting. If these steps are considered, I believe mortality rates would be successfully mitigated to enhance the restoration footprint and success of massive coral species.

**Tables.****Table 1.** Results from the Generalized Linear Model used to model the probability of mortality of coral outplants in each experiment,

	N	P-value
<b><u>Acropora Protection</u></b>		
Treatments	3	0.00557
Plots	3	0.11152
Survey Period	3	< 2.3E-16
<b><u>Predator Exclusion</u></b>		
Treatments	4	<2.2E-16
Plots	3	0.06281
Survey Period	3	<2.2E-16
<b><u>Size Influence</u></b>		
Treatments	2	0.01371
Plots	3	0.17954
Survey Period	3	<2.2E-16
<b><u>Genotype Influence</u></b>		
Genotypes	6	<2.2E-16
Survey Period	3	1.495E-08

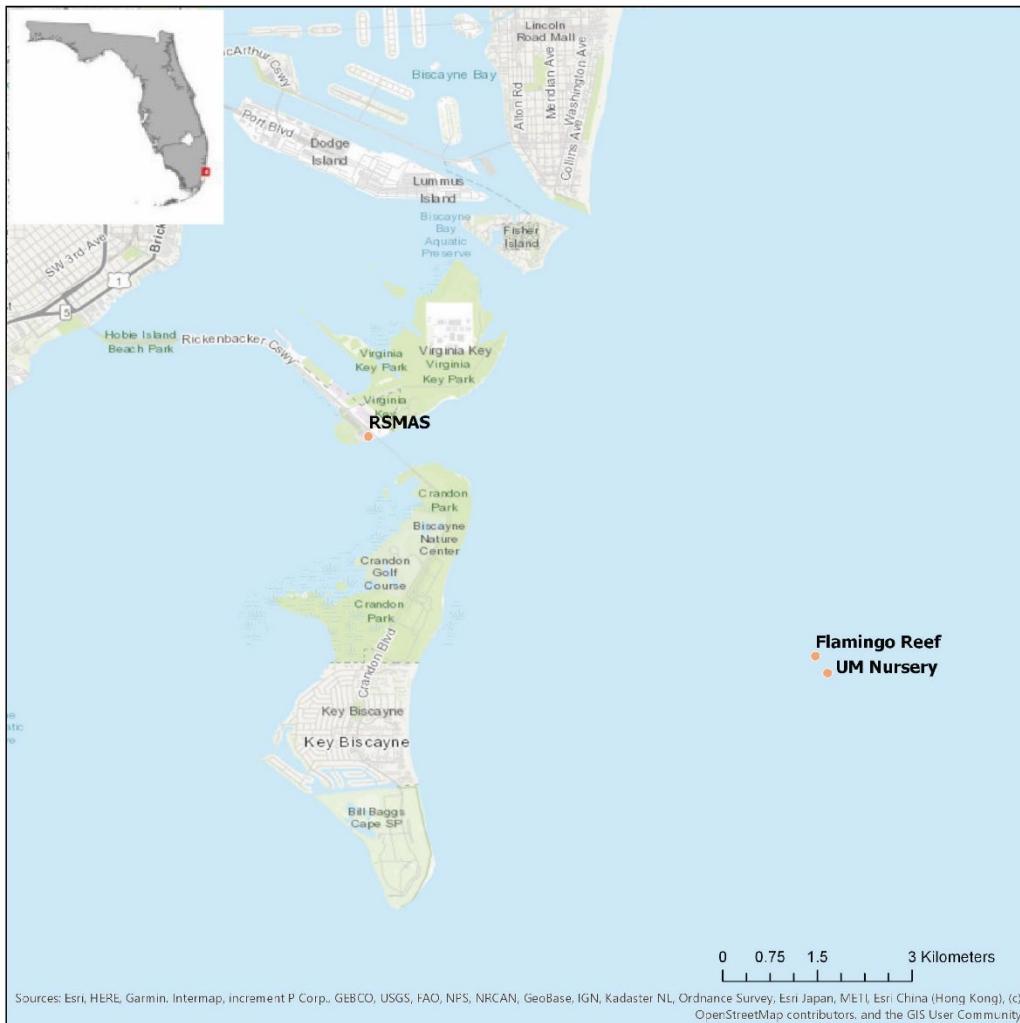
**Table 2.** List of fish species seen interacting with coral outplants during video surveys.

Scientific Name	Common Name
<i>Chaetodon striatus</i>	Banded Butterflyfish
<i>Chaetodon capistratus</i>	Foureye Butterflyfish
<i>Stegastes partitus</i>	Bicolor Damselfish
<i>Stegastes fuscus</i>	Dusky Damselfish
<i>Scarus guacamaia</i>	Rainbow Parrotfish
<i>Balistes capriscus</i>	Gray Triggerfish
<i>Halichoeres bivittatus</i>	Slippery Dick
<i>Halichoeres garnoti</i>	Yellowheaded Wrasse
<i>Halichoeres maculipinna</i>	Clown Wrasse
<i>Thalassoma bifasciatum</i>	Blueheaded Wrasse

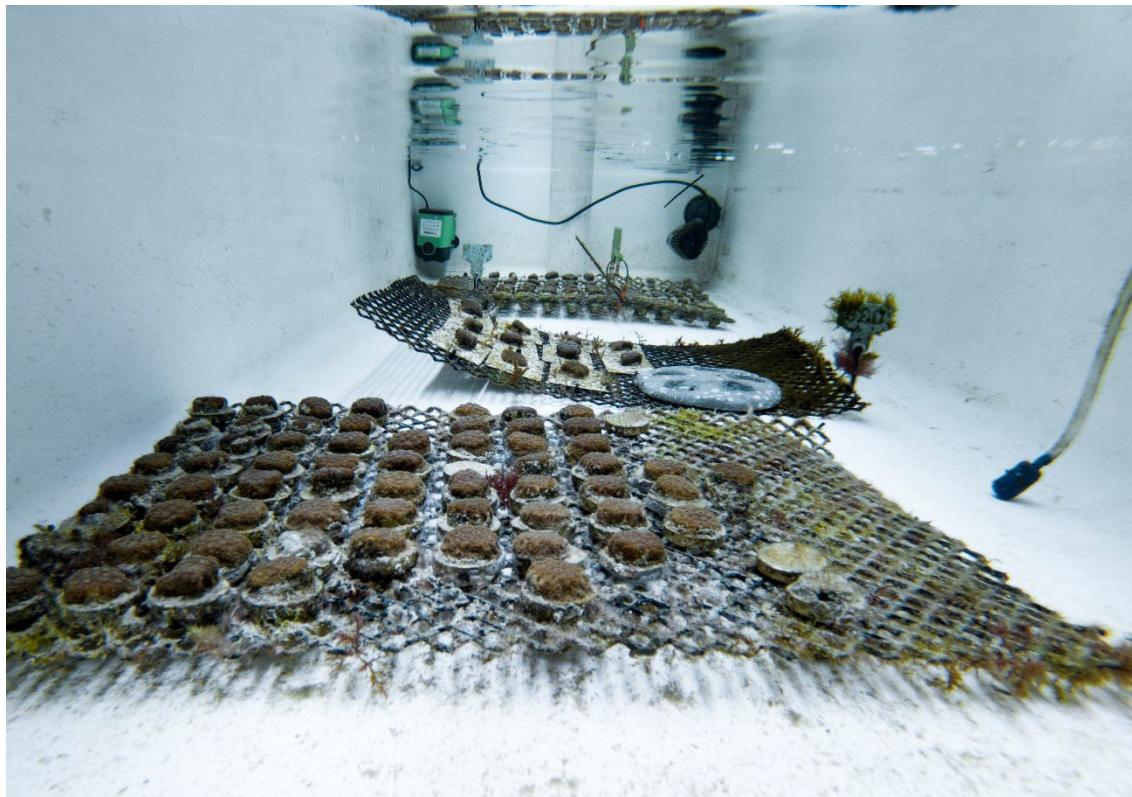
**Figures.**



**Figure 1.** Evidence of predation on an *Orbicella faveolata* fragment 7 days after outplanting.



**Figure 2.** Map of University of Miami Coral Nursery and Flamingo Reef.



**Figure 3.** *Orbicella faveolata* fragments mounted onto ceramic plugs.



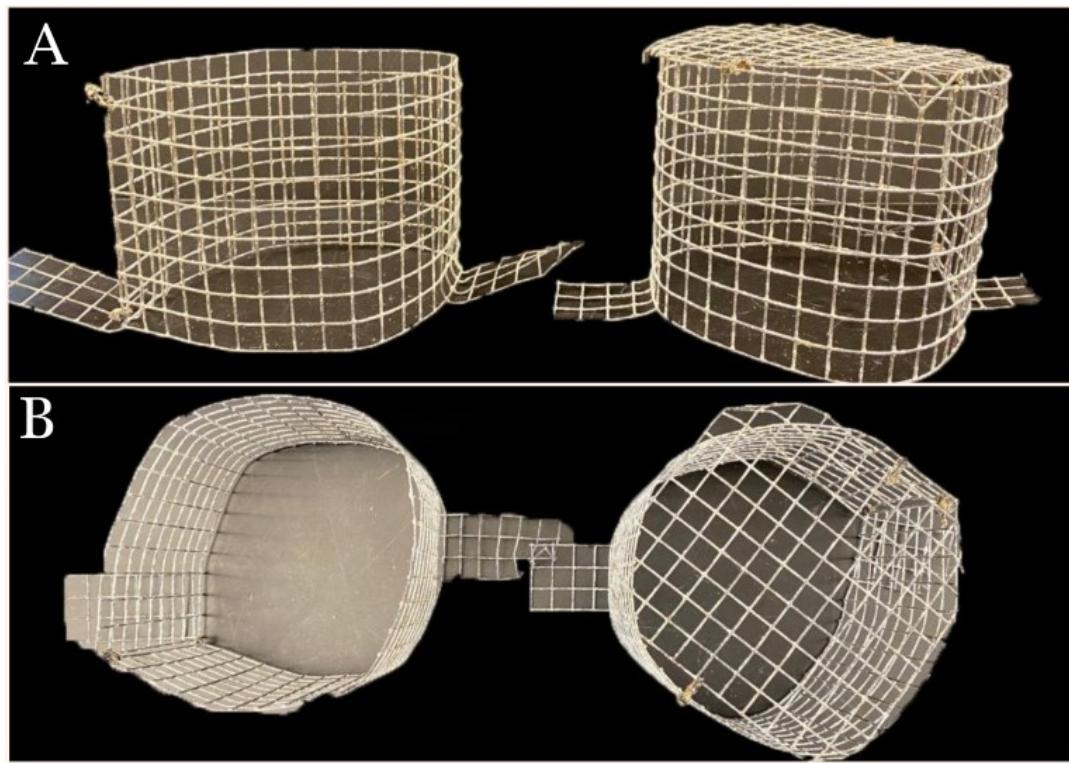
**Figure 4.** Landscape view of staghorn coral restoration plot at Flamingo Reef.



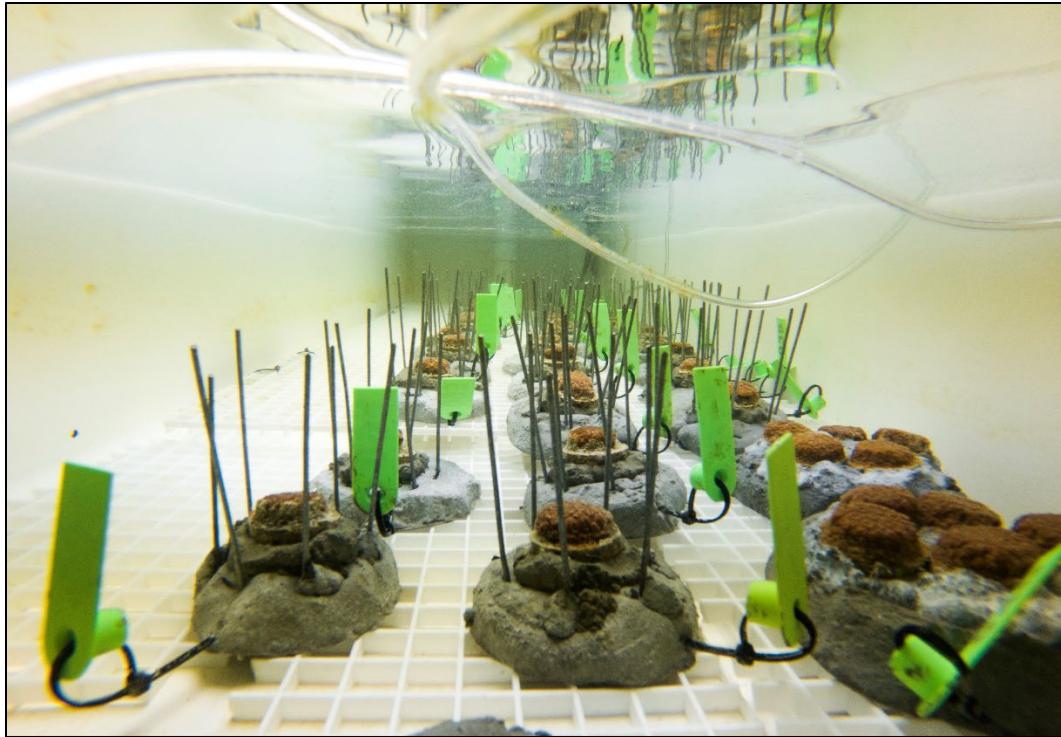
**Figure 5.** *Orbicella faveolata* fragment outplanted directly adjacent to a staghorn colony.



**Figure 6.** *Orbicella faveolata* outplants placed 0, 25, and 50 cm away from a staghorn colony.



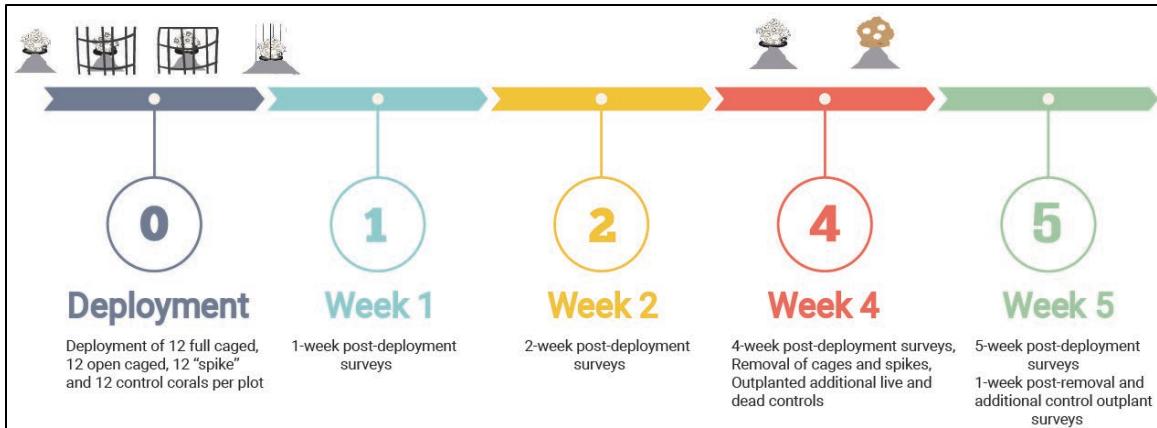
**Figure 7.** Open (left) and closed (right) cages made of galvanized steel mesh. (A) Horizontal view and (B) vertical view of cages.



**Figure 8.** Cement pucks with spikes and *Orbicella faveolata* fragments. Plastic numbered tags were used to track individual corals throughout the experiments.



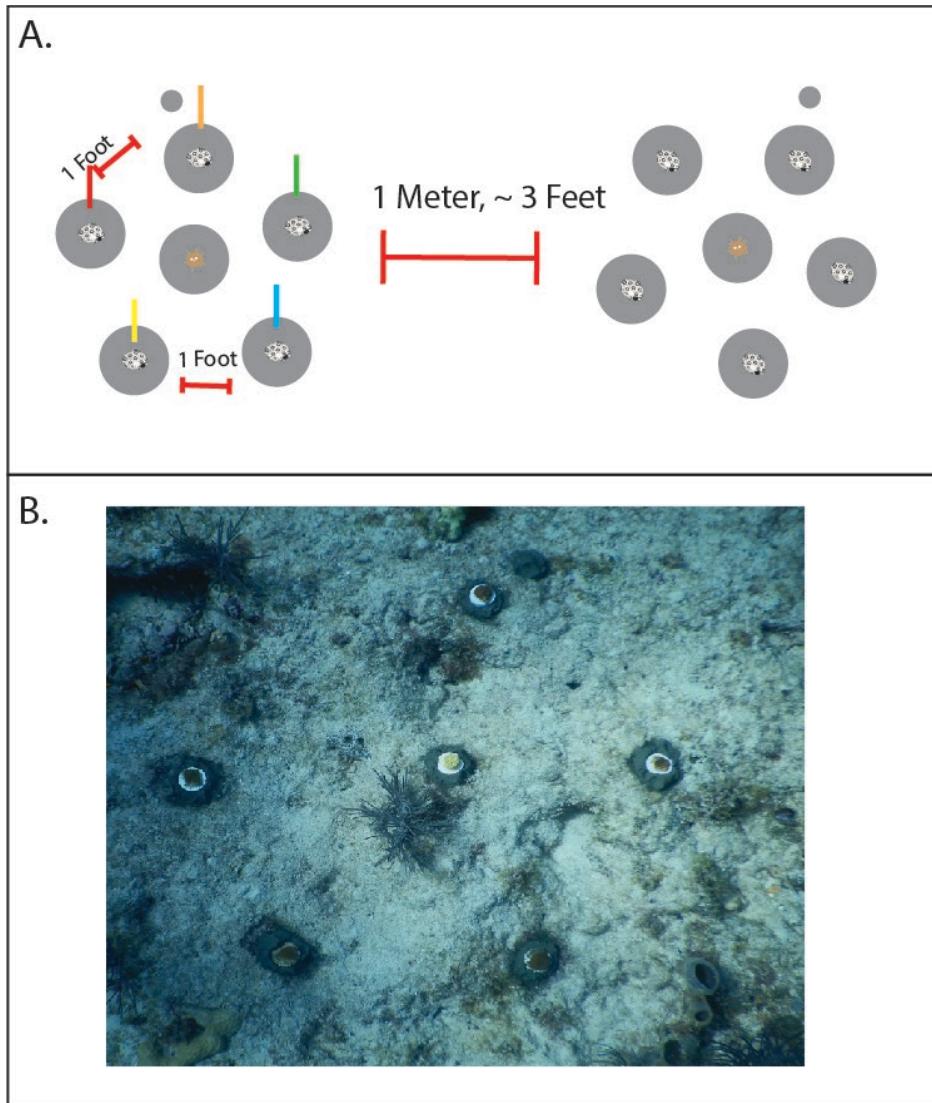
**Figure 9.** *Orbicella faveolata* fragment outplanted with no physical protection.



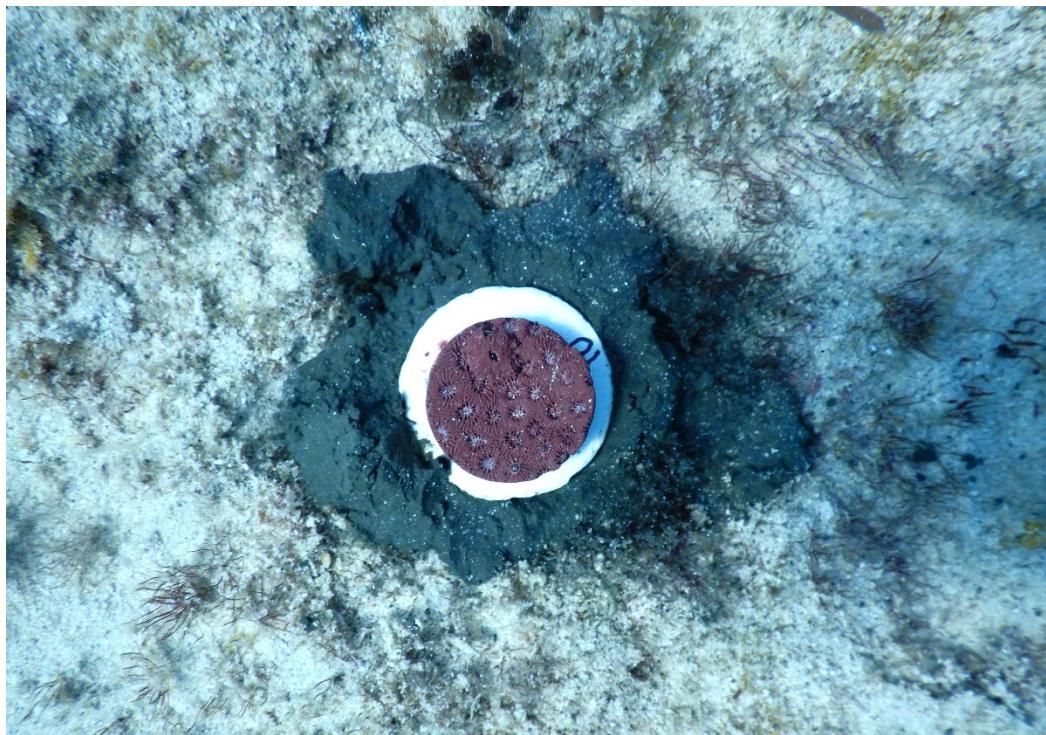
**Figure 10.** Timeline of Predator Exclusion experiment.



**Figure 11.** Five *O. faveolata* corals outplanted as a cluster ( $25 \text{ cm}^2$ ) to encourage fusion and resemble a larger coral colony.



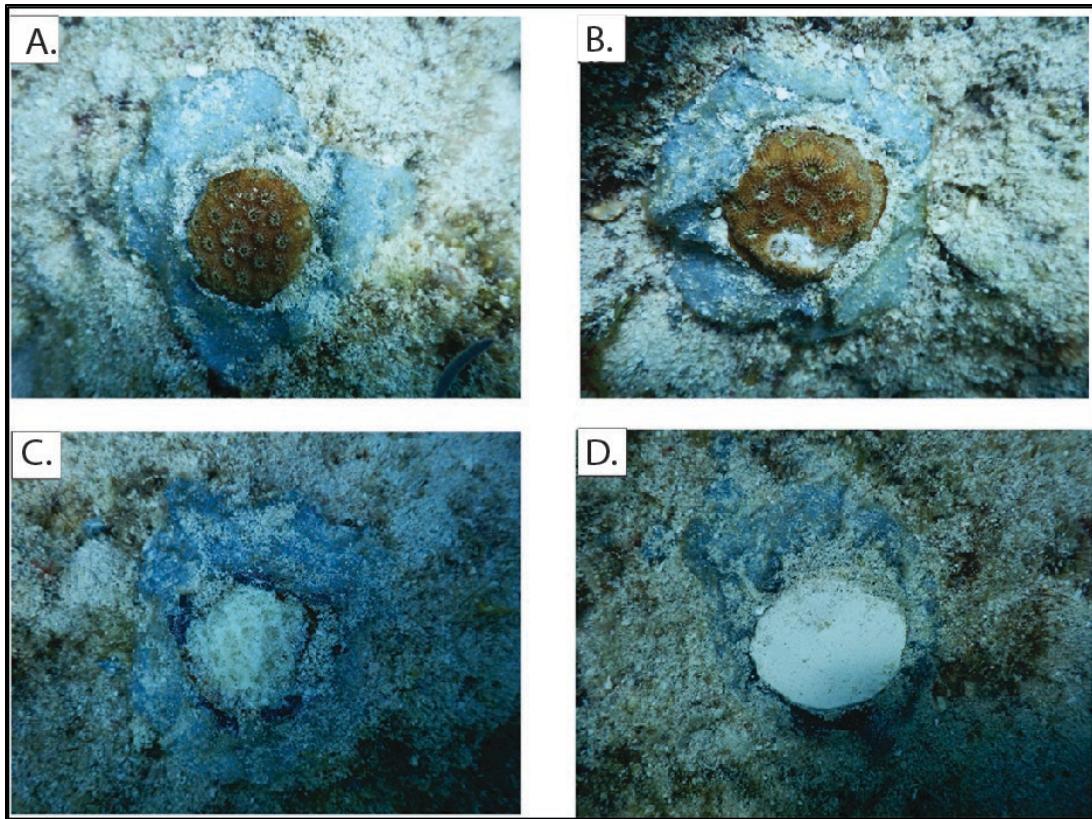
**Figure 12.** A. Layout of genotype outplants. B. Group of *Orbicella faveolata* outplants attached to reef floor with cement.



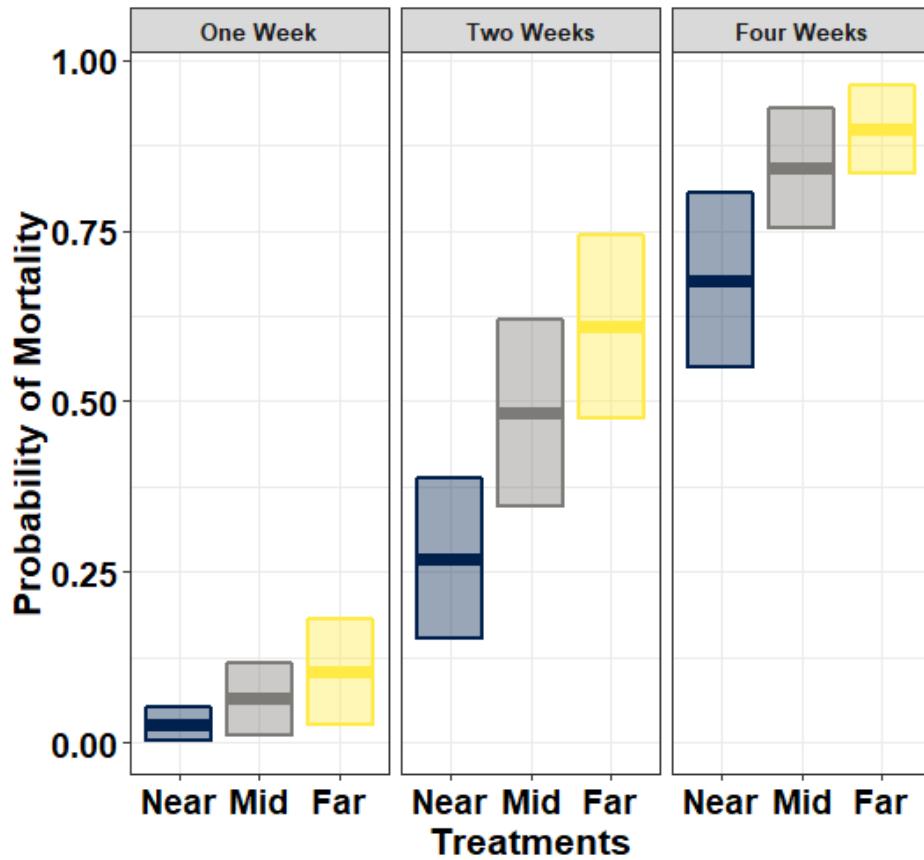
**Figure 13.** Dead *O. faveolata* fragment outplant painted with nail polish to mimic a live coral used to test fish territorial behavior.



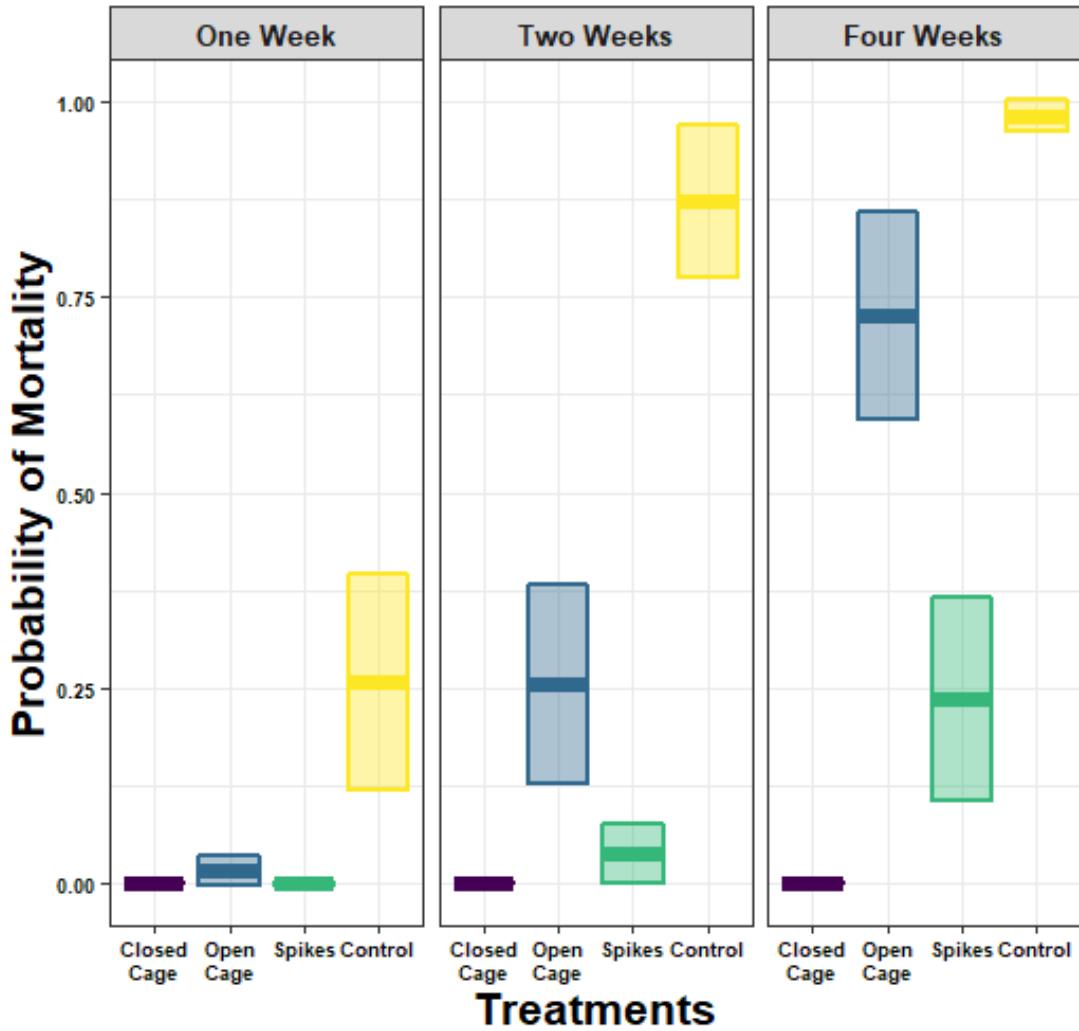
**Figure 14.** Video camera in PVC housing with red light attached used to record fish interactions with coral outplants.



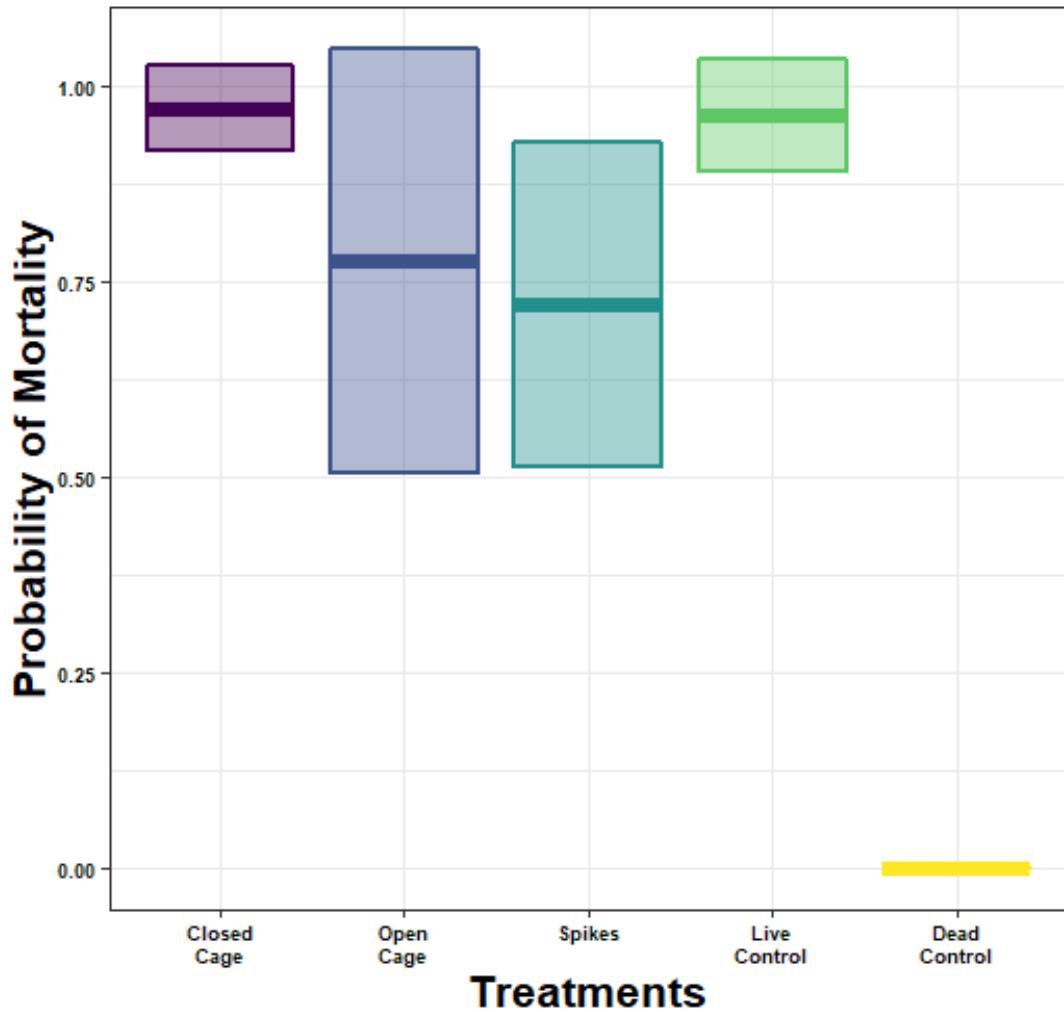
**Figure 15.** Photos depicting the four levels of predation observed. a) Healthy outplant with no predation (b) Outplant with partial predation (c) Outplant with all tissue removed (d) Outplant completely removed from ceramic plug.



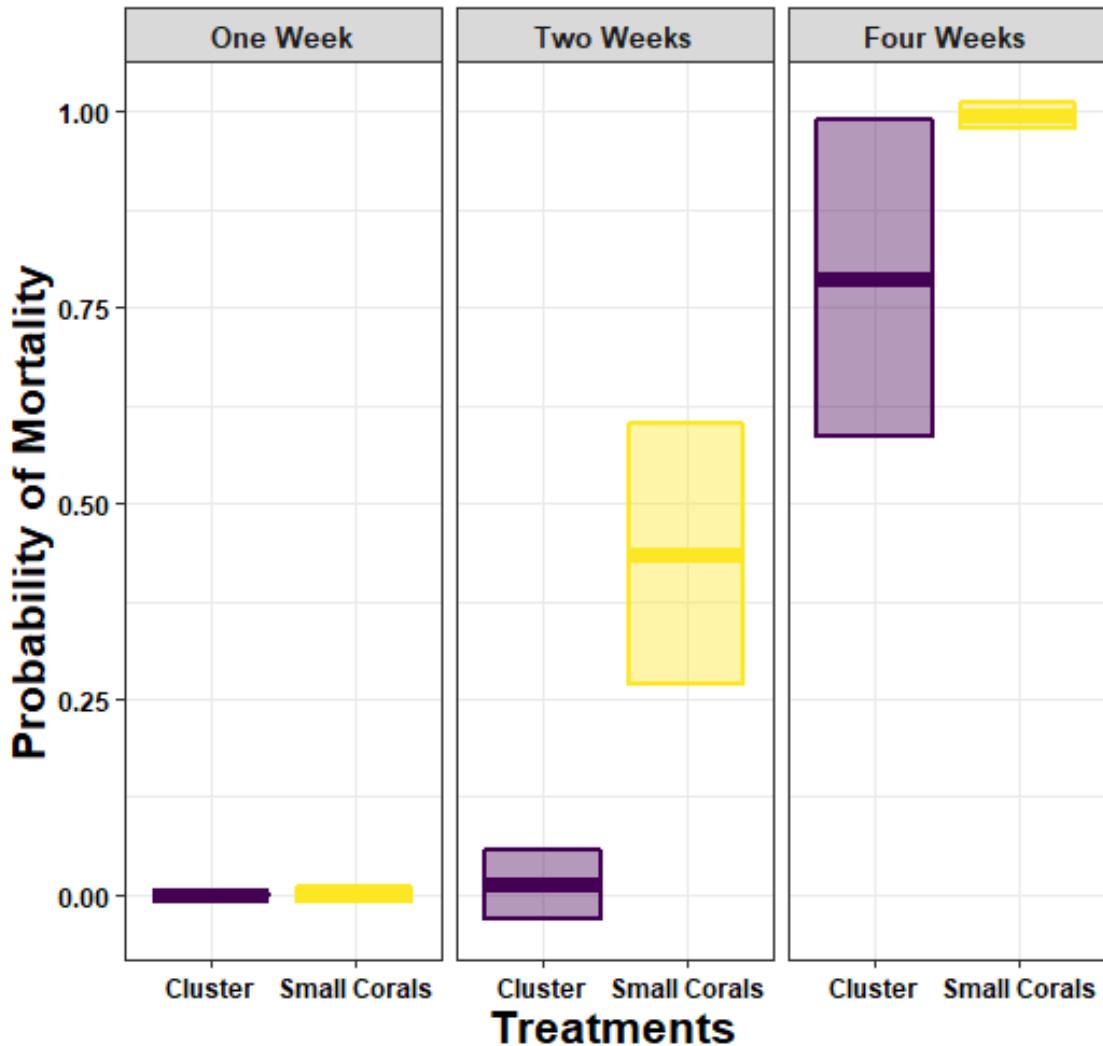
**Figure 26.** Probability of mortality by fish in Protection by *Acropora* experiment based on treatment and time estimated using a binomial GLM. Near, mid, far indicate adjacent, 25 cm away and 50 cm away from staghorn, respectively. Bars indicate GLM fitted values (center lines) and 95% confidence intervals. Tukey pairwise test comparisons: Near ≠ Mid = Far



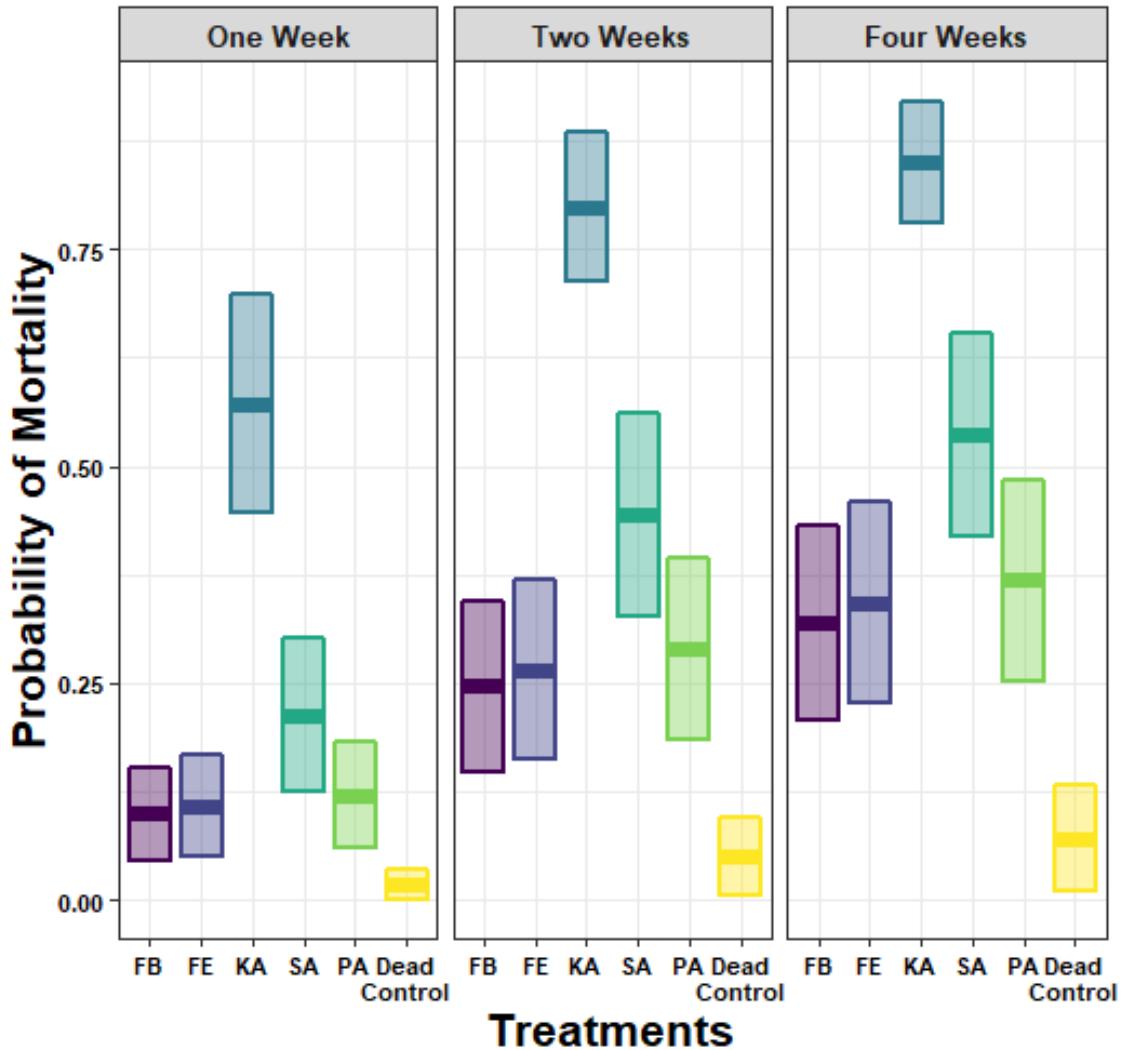
**Figure 37.** Probability of mortality by fish in Predator Exclusion experiment based on treatment and time estimated using a binomial GLM. Bars indicate GLM fitted values (center lines) and 95% confidence intervals. Tukey pairwise test comparisons: Open Cage  $\neq$  Spikes  $\neq$  Controls  $\neq$  Closed Cage.



**Figure 48.** Probability of removal by fish in Predator Exclusion experiment based on treatment and time estimated using a binomial GLM for the post protection removal period. Bars indicate GLM fitted values (center lines) and 95% confidence intervals. Tukey pairwise test comparisons: Dead Control  $\neq$  Closed Cage = Live Control = Spikes = Open Cage.



**Figure 19.** Probability of mortality by fish in Size Influence experiment based on treatment and time estimated using a binomial GLM. Bars indicate GLM fitted values (center lines) and 95% confidence intervals. Tukey pairwise test comparisons: Clusters ≠ Small corals. One week = two week ≠ four weeks.



**Figure 50.** Probability of mortality by fish in Genotype Influences experiment based on average mortality, treatment and time estimated using a binomial GLM. Bars indicate GLM fitted values (center lines) and 95% confidence intervals. Tukey pairwise test comparisons: Dead Control  $\neq$  KA  $\neq$  PA = SA = FB = FE. One week  $\neq$  Two weeks = Four weeks.

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